FARMING OF CORDGRASS, SPARTINA ALTERNIFLORA LOISEL., BY FIDDLER CRABS, UCA RAPAX (SMITH) (DECAPODA: OCYPODIDAE)

BY

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Abstract of Dissertation Presented to the Graduate School
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FARMING OF CORDGRASS, SPARTINA ALTERNIFLORA LOISEL. BY FIDDLER CRABS, UCA RAPAX (SMITH) (DECAPODA: OCYPODIDAE)

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The fiddler crab Uca rapax is a food limited detritivore that feeds on decaying cordgrass (Spartina alterniflora) in the salt marsh. Crab burrowing activity stimulates cordgrass growth, and thereby indirectly enhances their food supply. Fiddler crabs may dig more burrows than they require for their protective and physiological needs. There may be a selective advantage in digging "excess" burrows, because of the indirect benefit of enhancing food supply and decreasing the competition for food. The hypothesis that fiddler crabs "farm" cordgrass was examined by (a) comparing burrow and crab density in a salt marsh, (b) manipulating burrow density to test whether fiddler crabs dig burrows in excess of the ones available, and (c) manipulating food availability to test whether crabs adjust their burrowing activity in response to food. Results showed that (a) there were more burrows than fiddler crabs, (b) crabs dug new burrows despite the presence of unoccupied burrows, and (c) their burrowing activity varied inversely with food availability. Food availability affected the rate of burrowing by females and males equally, but had a stronger effect on burrowing by small crabs than on that of large crabs. Thus, small crabs may be more sensitive to food limitation, and may be more efficient in "farming" cordgrass.

INTRODUCTION

Organisms may regulate or control other trophic levels by establishing interactions with each other and feedback relationships (Kitchell *et al.*, 1979; Montague *et al.*, 1981; Patten and Odum, 1981). In salt marshes, fiddler crabs have a large impact on cordgrass, *Spartina alterniflora*: their burrowing activities, bioturbation and fecal pellet production increase the growth of *Spartina*, resulting in an increased food supply in the form of microorganisms that colonize the grass when it dies and decays (Montague, 1980a, 1980b; Katz, 1980; Bertness, 1985). These crabs are food limited in the salt marsh (Genoni, 1985). Selection may favor activities and by-products that would decrease food limitation, such as, perhaps, burrowing activity. Fiddler crabs may be said, then, to "farm" salt marsh grass, like some earthworms "farm" plants in their habitat (Darwin, 1881), an indirect effect *sensu* Wilson (1980).

Burrows have a number of direct advantages for fiddler crabs: they function as shelters from predators and environmental extremes; provide water for physiological needs; and are sites for reproduction (Crane, 1975; Hyatt and Salmon, 1977; Young and Ambrose, 1978; Ringold, 1979). They may serve other presently unidentified functions. If fiddler crabs dig more burrows than they require for these needs, then the benefit of an increased food supply may not be merely a by-product of their burrowing activity (Montague, 1980a).

The hypothesis that the fiddler crab *Uca rapax* (Smith) farms cordgrass was examined by (a) measuring and comparing natural burrow density and crab density; (b) manipulating burrow density to test whether fiddler crabs tend to dig burrows in excess of the ones available; and (c) manipulating food levels to test whether such excess burrowing may represent farming.

The prediction was made that the burrow/crab ratio would be >1. Since fiddler crabs are food limited, and since burrows enhance their food supply, they may tend to excavate burrows or burrow branches in excess of a ratio of one burrow available per crab. If they do so in spite of the comparatively high energy investment required to burrow in a muddy substrate, one explanation may be that they farm *Spartina*. Fiddler crabs sometimes forage in parts of the marsh with no burrows (Montague, 1980a), suggesting that excess burrows are not only for predator escape. The possibility that excess burrows are only for reproduction is equally unlikely, because males may not be able to defend several burrows (where females incubate their eggs; Crane, 1975). To test against these and other possibilities (e.g. parasite avoidance, reduced time constraints, physiological stress, etc.), food levels were manipulated. If fiddler crabs are capable of adjusting their burrowing activity to food availability, burrowing activity was predicted to be lower if food is abundant and higher if food is scarce.

The species used in this study is *Uca rapax*. Work on *Uca pugnax* will be referred to because of its similarity to *U. rapax*.

METHODS

Burrow/crab Ratios in the Salt Marsh

A sampling of Uca rapax population density, sex ratio, size class distribution, and burrow density was done during Summer 1985 in an intertidal salt marsh at Matanzas Inlet, St. Johns County, Florida (29°45'50" N, 81°17'20" W). The vertical tidal range is ~1.9 m, and the distribution of vegetative zones is fairly distinct. The site is dominated by a medium growth form (~50 cm tall) of cordgrass, Spartina alterniflora Loisel. (~140 shoots/m^2). The sediment is fine mud with a small sandy fraction.

To identify burrow/crab ratios, I used sampling techniques as described by Frey et al. (1973), Wolf et al. (1975), and Ringold (1979). An area of 12 by 12 m, which was apparently homogeneous in Spartina height and density, Uca density, and physical factors, was chosen. It was divided into 0.5 by 0.5 m quadrats and marked permanently with dowels. Between 9 June and 6 September, 17 quadrats were chosen by the simple random method (Snedecor and Cochran, 1980) for measurement of Uca and burrow density. Each quadrat was enclosed with corrugated fiberglass panels while water still covered the substrate and most crabs were in their burrows (Wolf et al., 1975; Genoni, 1985). At low tide, grass shoots within the quadrat were clipped near the substrate. Shoots were counted and later dried 48 h at 70° C and weighed to the nearest 0.1 g with an Ohaus trip balance. To determine the characteristics of each burrow and identify resident crabs, burrow openings were marked with numbered sticks, and burrow casts were taken with polyester resin (Dembowski, 1926; Shinn, 1968). The resin caused resident crabs to escape. Their sex was noted and their carapace breadth was measured to the nearest 0.05 mm with Vernier calipers. Because some burrows are kept plugged by resident crabs at any time (Crane, 1975), this procedure was repeated on the next two days with newly opened burrows. Association of burrows with structural elements in the substrate (grass stems or mussel shells, Geukensia demissa) was estimated by scoring burrows as either occurring on bare substrate (>2 cm from a stem or mussel) or structure-associated (<2 cm) (Bertness and Miller, 1984).

On the third day, burrow casts were removed and their depth, angle from the substrate surface, diameter and configuration were noted. To sample root mat density, a 20-cm deep sediment core was taken with a PVC tube (5.2 cm in diameter). To sample water content and organic content, two 7-cm deep cores were taken with a PVC tube (3.0 cm in diameter). In the laboratory, the larger sediment core was sieved through a 0.5 mm mesh, and the roots were dried 48 h at 70° C and weighed to the nearest 0.01 g with a Mettler H8 analytic balance. One smaller core was weighed wet, dried 48 h at 110° C and weighed again to determine the water content. The upper 0.5 cm from the other core was weighed wet, dried 48 h at 70° C, then weighed dry and left for 4 h in a Sybron Corp. Thermolyne 10500 muffle furnace at 500° C. It was then rehydrated, dried again, and weighed. The ash-free dry weight was determined and the organic content was estimated as the weight of the fraction lost in the ashing (Paine, 1971).

Total counts of burrow and crab density, and *Spartina* biomass and density, were pooled for all 17 quadrats, whereas data from subsamples were averaged over all quadrats.

Effects of Burrow Density and Food Availability

In a manipulative experiment in the laboratory, the effect of food availability and burrow density on burrowing activity of *U. rapax* was tested. Two sets of four circular arenas were built, each consisting of a plastic pail on top of which a sheet of metal was riveted to make a funnel with walls inclined at a 45° angle. The metal was lined with plastic and topped with a 10-cm strip of aluminium flashing that crabs could not climb. The arenas were filled with sandy mud (collected from a creek in the salt marsh) 45 cm deep, with an upper diameter of 52 cm and a surface area of 0.21 m^2. Results from the field study were used to determine the initial conditions used in the arenas. At the beginning of each trial, complete randomization (Snedecor and Cochran, 1980) was used in assigning each arena to one of four treatments: (1) low food abundance and low burrow density, (2) low food and high density, (3) high food and low density, and (4) high food and high density. This 2^2 factorial experiment was replicated in 17 trials, between April 7 and September 14, 1987. The following responses were predicted: burrowing activity should be highest in treatment (1), both to stimulate food and for other needs (protective, reproductive and physiological); intermediate in (2), to stimulate food; and in (3), to meet other needs; and lowest in (4).

Food treatments consisted of 0 g and 11 g, respectively, of Purina Fly Larvae Medium added to each arena. For a 7-day trial, the high value corresponds to 19 kcal/(m^2x day), i.e. about twice the highest estimate of average energy consumption of fiddler crabs calculated by Cammen _et al._ (1980) (3522 kcal/(m^2x yr) or 9.7 kcal/(m^2x day)). The arenas where food was not added contained some organic matter mixed with the sediment, as evidenced by the feeding response of crabs. This behavior is mediated by chemoreceptors in the minor chelae (Robertson _et al._, 1980, 1981). To measure the organic content of the upper 0.5 cm of sediment, cores (2.7 cm in diameter) were taken from each arena before each trial, and ash-free dry weight was determined as outlined above.

Initial burrows (43 and 64 per arena, for high and low density treatments) were made by pushing dowels 15 cm into the substrate, at angles of 60°-80°. Thus, burrow densities were $205/m^2$ and $302/m^2$. Burrow openings were marked with _Spartina_ stems cut to 10 cm, on which numbered tags were stapled. Additional stems were placed in the low-density arenas to achieve similar stem densities.

Uca rapax were captured at the Matanzas Inlet site and 43 individuals were distributed into each arena. The sex ratio and size class distribution in each arena were similar to those observed in the sampling study, with the exception that no crabs <6 mm in carapace breadth were used, due to the difficulty of surveying their burrows. The following size classes were used, as determined by carapace breadth: 6-8, 8-11, 11-15, and >15 mm. Because competition for burrows of adequate size may be stronger for larger crabs (Bertness and Miller, 1984), the diameter of initial burrows was varied to match crab carapace length (crabs enter their burrows sideways). Crabs were left in the arenas 4.0-7.5 days, at 25°C, in a laboratory equipped with windows and with fluorescent lights set on a timer simulating the sunrise-sunset rhythm. Thus, the natural photoperiod was supplemented by an artificial photoperiod. Arenas were separated by blinds from the rest of the laboratory. The sediment was maintained wet by additions of 50 % seawater.

The following parameters were used to describe fiddler crab burrowing activity: the number of new unbranched and branched burrows, the amount of excavated sediment, and the percent of time allocated to burrowing (Katz, 1980; Montague, 1980a). At the end of each trial, excavated material was collected, dried 48 h at 70° C, and weighed to the nearest 0.01 g. Newly excavated burrows were marked. I noted the presence of half-domes of mud (or "shelters"; Zucker, 1974) constructed by some individuals on burrow openings. To determine the characteristics of each burrow and identify resident crabs, burrow casts were made with latex concrete (Christy, 1982). The concrete caused resident crabs to escape. Their sex and carapace breadth were noted. This procedure was repeated with newly opened burrows on the next two days. Burrow casts were removed and their depth, diameter and configuration were noted.

Association of burrows with structural elements (grass stems) was estimated as described for the field study.

Counts of new unbranched and branched burrows and measurements of excavated sediment were divided by the duration of each trial in days. These variables, burrow depths, and branching ratios (defined as the ratio of the number of branches to the number of burrows) were analysed by 2^2 factorial ANOVAs for tests of the effects of food and density treatments and their interaction. The assumption of normality was tested by two-tailed t-tests on skewness and kurtosis; the assumption of homogeneity of variances was tested by Levene's one-way ANOVA. If these assumptions were not met, factorial ANOVAs were done on log-transformed data (the assumptions were tested again). Comparisons between treatments of the percent of unbranched burrows were done by X^2 tests of independence.

Comparisons of responses to initial burrow density and to food availability were also made for each sex and each size class. Crabs of each sex or size class may not be equally sensitive to food supply, because of different foraging efficiencies or food assimilation, or because dominance by one sex or by larger crabs may limit food availability to other crabs (Hyman, 1922; Crane, 1975). Comparisons of shelter building between sexes and size classes was done by X^2 tests of independence.

To investigate time allocation to different activities, including burrowing, crabs were marked individually with numbered plastic tags affixed with cyanoacrylate glue to their carapace. For every arena, activities of individual crabs were recorded from circular visual scans. Successive observations were made every 10 s for 15 min. This procedure was repeated 1 to 4 times, on different days, during 7 of the trials. The percent of the total time allocated to various activities was estimated from the frequencies of their occurrence among the observations (scan sampling; Altmann, 1974). Activities were grouped as follows: standing still (motionless), walking, eating, cleaning, agonism (combat and chasing), display and courtship, and burrow construction and maintenance. General comparisons between treatments of the fraction of time allocated to various activities were done by X^2 tests of independence across all treatments, for all crabs, and for each sex and size class. Comparisons of the fraction of time allocated to certain activities (e.g. burrowing) were done on arcsine-transformed data by factorial ANOVAs. An index of relative activity of crabs of each sex or size class was calculated from the frequency of sightings observed and expected from the sex ratios and size class distribution in the arenas. Activity levels were compared by X^2 tests of indepedence.

Statistical analyses were done on an IBM 3081-D32/3090-200 mainframe computer at the North Eastern Regional Data Center of the State University System, Gainesville, FL, using the Statistical Analysis System (SAS Institute Inc., 1985a, 1985b) and the Biomedical Data Program P-Series (Dixon, 1985).

RESULTS

Burrow/crab Ratios in the Salt Marsh

At the study site, the sediment was sandy mud, and sediment water was 64.59 % of wet weight (s.d.=3.16, N=17). Organic matter in the upper 0.5 cm was 9.05 % (s.d.=2.64, N=12). Spartina shoot density was 138.1/m^2 (N=17) and standing stock was 269.52 dry g/m^2 (N=15). The root mat (roots and rhizomes), between 0 and 20 cm, was 0.11 dry g/ml (s.d.=0.04, N=15).

There were 212 burrows/m^2 (N=17) and 156 fiddler crabs/m^2 (N=17). Thus the burrow/crab ratio was 1.36. Sex ratio (M/F) was 0.79 (N=565 crabs). Size class distribution was 31.0 % (carapace breadth <6 mm), 20.6 % (6-8), 17.0 %(8-11), 23.2 % (11-15) and 8.2 % (>15) (N=548 crabs).

Burrows were significantly associated with structural elements of the substrate; using a value of 70.0 % available bare substrate (Bertness and Miller, 1984), a conservative estimate considering the shoot density at the study site, burrows occurred near stems or mussels more frequently than expected by chance alone (37.0% of all burrows, X^2=29.90, df=1, $p<0.0001$, N=1284). Burrow angles from the substrate ranged from 30° to 90° but most (64.8 %, N=213 burrows) were at an angle between 60° and 80°. Most burrows (89.0 %, N=427) were unbranched and J-shaped, their main shaft being usually straight but sometimes comprising one or more turns. Other configurations (11.0 % of the burrows) reflected branching or interconnection of burrows, and might be grouped under the designations of Y, U, and H configurations (Allen and Curran, 1974). They had (in decreasing frequency of occurrence) 2, 3, or 4 branches, most of which led to an opening. Burrow depth (projected against an imaginary vertical plane, i.e. not taking into account burrow angle) ranged from 1 to 11 cm (N=94).

These data, to the extent that they were used to set up experimental arenas, are summarized in Table I.

Effects of Burrow Density and Food Availability

Fiddler crabs occupied and remodeled the artificial burrows, and dug additional burrows and branches. Few were seen walking along the walls or burrowing against them. Fiddler crabs dug, on average, 34.99 ± 13.30 new burrows per trial (N=68). Of these, 19.88 ± 10.52 were unbranched burrows. Thus, the branching ratio for all burrows was 1.25 ± 0.58 (N=3340). Another useful variable is the count of all burrows occupied or maintained to the end of each trial, excluding abandoned burrows, which usually collapsed: there were 8.86/day ± 1.28 maintained burrows, 11.33/day ± 1.68 new branches and 2.44/day ± 1.08 branches added to initial burrows. The burrowing activity removed 70.31 dry g/day of sediment (s.d.=17.82), or an average of 1.64 dry g/crab/day. The fraction of time allocated to the various activities is presented in Table IIa. The fraction allocated to burrowing was 5.9 % (N=4628 observations).

Table I. (a) Summary of environmental and population characteristics observed at the salt marsh site and used as initial conditions in the experimental arenas; (b) Matching of initial burrow diameter with crab size. CB=carapace breadth.

(a)

Variable	Field study	Arenas
Sediment type	Sandy mud	Sandy mud
Sediment water	64.6 %	55.4 %
Burrow density	$212/m^2$	High: $302/m^2$ (64/arena) Low: $205/m^2$ (43/arena)
Uca density	$156/m^2$	$205/m^2$ (43/arena)
Burrow/crab ratios	1.36	High: 1.5 Low: 1.0
Burrow angles	64.8 % 60°-80°	60°-80°
Burrow configurations	89.0 % J-shaped	Straight
Uca sex ratio (M/F)	0.79	0.79
Uca size-class distribution, by sex		
CB 6 - 8 mm	18.7% F, 13.7% M	18.6% F, 14.0% M
CB 8 - 11 mm	13.7 10.1	14.0 9.3
CB 11 - 15 mm	17.3 11.5	16.3 11.6
CB >15 mm	6.5 8.6	9.3 7.0
Food available to *Uca*	9.7 kcal/(m^2 x yr)(1)	High: 19.0 kcal/(m^2 x yr) Low: 2.6 kcal/(m^2 x yr)

(b)

Size class	Carapace length (2)	Burrow diameter
CB 6 - 8 mm	5.44 mm	5.50 mm
CB 8 - 11 mm	7.34 mm	7.40 mm
CB 11 - 15 mm	9.87 mm	9.90 mm
CB > 15 mm	11.46 mm	12.20 mm

(1) Cammen *et al.* (1980).

(2) CL was predicted on the basis of a regression of carapace length against carapace breadth. The morphometric analysis of carapace and chela measurements is presented in the Appendix.

Table II. Time allocation (%) to various activities by *Uca rapax*; (a) all crabs, (b) each sex and (c) each size class.

	Still	Eat	Walk	Burrow	Clean	Agonism	Display	N	Test	df	Significance
(a)	36.7	36.0	11.7	5.9	5.3	3.0	1.3	4628			
(b)								4493	$X^2=131.69$	6	$p<0.0001$
Females	35.5	38.3	12.8	8.3	4.5	0.7	-	1722			
Males	37.2	35.2	10.9	4.1	6.0	4.4	2.2	2771			
(c)								4536	$X^2=168.53$	6	$p<0.0001$
Size class 1	23.4	55.2	5.2	8.4	6.8	0.9	-	440			
2	39.3	37.4	10.9	7.0	3.3	1.4	0.6	905			
3	36.9	35.6	12.6	5.0	5.5	2.8	1.6	1777			
4	39.8	29.8	12.5	5.3	5.5	4.7	1.8	1414			

Configurations were of the J, Y, U and H types, and sometimes more complex. Most shafts were straight, even those of newly dug burrows, and walls were smooth. Burrow depth was 5.63 ± 2.71 cm (N=2597, max.=20.0 cm). There were only 1.84 shelters per arena, on average (N=125). Burrows were significantly associated with structural elements (stems): using a calculated value of 75 % available substrate, burrows were adjacent to stems more frequently than expected by chance alone (28 % of burrows, X^2=5.05, df=1, p>0.025, N=634).

Water content of the sediment in arenas was 55.35 % (s.d.=5.43, N=27), which was lower than that of the salt marsh sediment. However this was the highest water content that allowed construction of artificial burrows. The organic matter present was 7.969 % (s.d.=1.690, N=55). Using a conversion of 0.323 kcal/(m^2x yr) for an organic fraction of 1 % calculated from data of Cammen et al. (1980), this value for low food treatments corresponds to 2.62 kcal/(m^2x yr).

Effect of initial burrow density

The interaction between initial burrow density and food availability was not significant for all variables examined by ANOVAs.

Some of the variables describing burrowing activity were affected by initial burrow density. Results are summarized in Tables III and IVa and Figure 1. The data shown in Table III are collapsed for the two levels of the burrow density treatment, but the value of F is for the main effect of burrow density in the factorial ANOVA. There were no differences between treatments in

Table III. Effect of initial burrow density on burrowing activity of *Uca rapax* (all crabs).

Variable	Low density	High density	Skewness	Kurtosis	Levene	N	Test	df	Significance	
All new burrows	39.63±11.76	30.06±13.24	NS	NS	NS	17	F=11.13	1	p<0.0014	
New unbranched burrows	24.74± 9.41	14.73± 9.19	NS	NS	NS	17	F=19.43	1	p<0.0001	
Maintained burrows (3)	8.62± 1.23	9.11± 1.31	p<0.001	NS	NS	16	F= 2.41	1	NS	(1)
New branches to initial burrows (3)	2.41± 1.06	2.48± 1.11	p<0.01	p<0.001	NS	16	F= 0.03	1	NS	(1)
Maintained branches (3)	11.09± 1.57	11.58± 1.79	p<0.001	p<0.001	NS	17	F= 1.50	1	NS	(1)
Branching ratio	1.27± 0.58	1.22± 0.58	p<0.0001	p<0.001	p<0.0001	3340	F= 9.21	1	p<0.0024	(1)
Burrow depth (cm)	5.57± 2.66	5.68± 2.76	p<0.0001	p<0.001	p<0.0001	2596	F= 1.25	1	NS	(1)
g excavated sediment (3)	70.91±19.23	69.68±16.48	NS	NS	NS	17	F= 0.08	1	NS	
% time burrowing	6.56 %	4.56 %	-	-	-	26	F= 1.72	1	NS	(2)

(1) Log-transformed data.
(2) Arcsine-transformed data.
(3) Divided by the duration of each trial in days.

Table IV. Response to initial burrow density of time allocation to various activities (%) by *Uca rapax*; (a) all crabs, (b) each sex and (c) each size class.

	Still	Eat	Walk	Burrow	Clean	Agonism	Display	N	Test	df	Significance
(a)								4628	$X^2=37.79$	5	$p<0.0001$
Low density	34.8	39.1	10.3	6.8	4.7	3.3	1.1				
High density	38.7	32.9	13.2	5.1	6.0	2.7	1.5				
(b)											
Females								1722	$X^2=29.96$	5	$p<0.0001$
Low density	32.6	42.9	11.3	9.1	3.3	0.8	-				
High density	38.7	33.2	14.4	7.4	5.7	0.6	-				
Males								2771	$X^2=18.24$	6	$p<0.006$
Low density	35.4	37.5	9.4	4.9	5.9	5.0	1.9				
High density	38.8	33.0	12.3	3.4	6.2	3.9	2.5				
(c)											
Size class 1								440	$X^2=8.23$	5	NS
Low density	19.3	56.3	5.3	9.1	8.0	1.5	-				
High density	28.8	53.7	5.1	7.3	5.1	-	-				
Size class 2								905	$X^2=14.93$	6	$p<0.021$
Low density	38.2	38.0	9.6	9.2	2.5	1.8	0.8				
High density	40.8	36.7	12.8	4.1	4.3	1.0	0.3				
Size class 3								1777	$X^2=35.55$	6	$p<0.0001$
Low density	33.4	41.8	12.0	4.3	5.2	2.3	0.5				
High density	39.9	30.4	13.2	5.6	5.8	2.6	2.6				
Size class 4								1414	$X^2=17.24$	6	$p<0.008$
Low density	40.0	30.8	10.3	6.7	4.8	5.1	2.5				
High density	39.6	28.8	14.5	4.0	7.3	4.4	1.3				

the number of maintained burrows, the number of branches added to initial burrows and branches of new burrows, the amount of excavated sediment, or burrow depth. However, in arenas with a lower initial burrow density, there were significantly more newly excavated burrows and the branching ratio was significantly higher; there was a trend for an increase in the fraction of time allocated to burrowing.

Differences between the reported fraction of time allocated to burrowing in Tables III and IVa (and in comparisons presented below) are the consequence of averaging across all treatments and averaging by factorial univariate analysis, respectively.

Effect of food availability

Some of the variables describing burrowing activity were affected by the food treatment. Results are summarized in Tables V and VIa and Figure 1. The data shown in Table V are collapsed for the two levels of the food treatment, but the value of F is for the main effect of food in the factorial ANOVA. There was no difference between treatments in the number of newly excavated burrows, the total number of maintained burrows, the amount of excavated sediment or the fraction of time allocated to burrowing. However, in arenas receiving no food additions, there were significantly more branches added to initial burrows and branches of new burrows, the branching ratio was higher, and average burrow depth was lower. In addition, time allocation to various activities was significantly affected by the treatment: in low-food arenas, crabs spent less time eating, wandered more

Table V. Effect of food availability on burrowing activity of *Uca rapax* (all crabs).

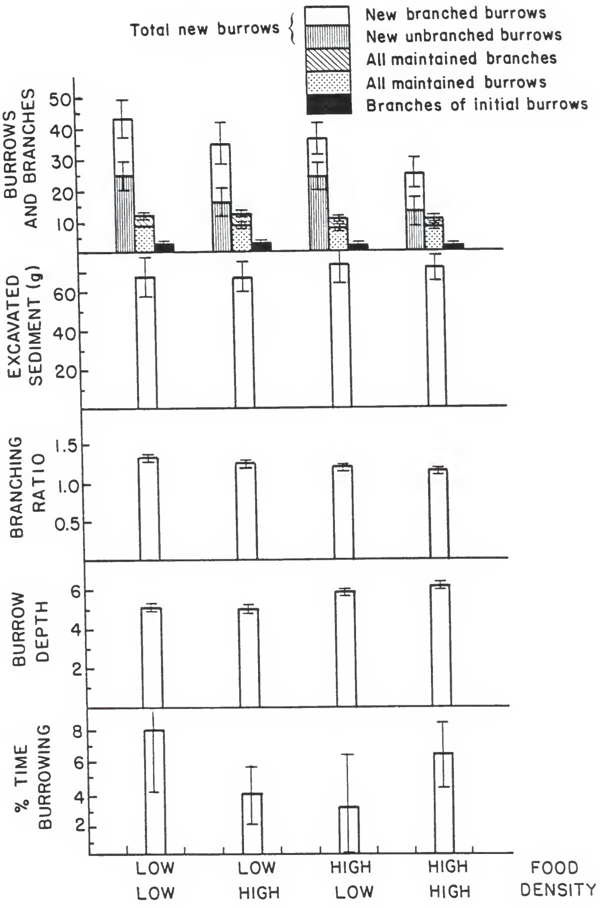
Variable	Low food	High food	Skewness	Kurtosis	Levene	N	Test	df	Significance
All new burrows	39.26±13.57	30.71±11.73	NS	NS	NS	17	F= 8.91	1	p<0.004
New unbranched burrows	20.88±10.20	18.88±10.89	NS	NS	NS	17	F= 0.78	1	NS
Maintained burrows (3)	8.92± 1.31	8.79± 1.27	p<0.001	NS	NS	16	F= 0.15	1	NS (1)
New branches to initial burrows (3)	2.96± 1.10	1.92± 0.78	p<0.01	p<0.001	NS	16	F=17.68	1	p<0.0001 (1)
Maintained branches (3)	11.90± 1.78	10.75± 1.38	p<0.001	p<0.001	NS	17	F= 8.36	1	p<0.005 (1)
Branching ratio	1.31± 0.62	1.19± 0.53	p<0.001	p<0.001	p<0.0001	3340	F=25.53	1	p<0.0001 (1)
Burrow depth (cm)	5.19± 2.38	6.08± 2.95	p<0.001	p<0.001	p<0.0001	2596	F=51.53	1	p<0.0001 (1)
g excavated sediment (3)	67.92±19.06	72.70±16.43	NS	NS	NS	17	F= 1.19	1	NS
% time burrowing	5.49 %	5.72 %	-	-	-	27	F= 0.25	1	NS (2)

(1) Log-transformed data.
(2) Arcsine-transformed data.
(3) Divided by the duration of each trial in days.

Table VI. Response to food availability of time allocation to various activities (%) by *Uca rapax*; (a) all crabs, (b) each sex and (c) each size class.

	Still	Eat	Walk	Burrow	Clean	Agonism	Display	N	Test	df	Significance
(a)								4628	$X^2=134.58$	6	$p<0.0001$
Low food	40.6	29.5	13.7	6.0	4.4	4.0	1.8				
High food	32.4	43.1	9.5	5.9	6.4	1.8	0.8				
(b)											
Females								1722	$X^2=35.43$	5	$p<0.0001$
Low food	39.4	31.9	14.2	9.2	4.0	1.2	-				
High food	31.7	44.4	11.4	7.4	4.9	0.2	-				
Males								2771	$X^2=103.53$	6	$p<0.0001$
Low food	41.4	28.4	13.1	3.9	4.6	5.7	2.9				
High food	32.2	43.2	8.3	4.3	7.7	3.0	1.3				
(c)											
Size class 1								440	$X^2=25.01$	5	$p<0.0001$
Low food	32.7	47.1	5.3	7.2	5.8	1.9	-				
High food	15.1	62.5	5.2	9.5	7.8	-	-				
Size class 2								905	$X^2=26.29$	6	$p<0.0001$
Low food	37.4	34.9	13.4	8.9	2.1	2.6	0.6				
High food	41.4	40.2	8.3	4.8	4.6	0.2	0.5				
Size class 3								1777	$X^2=55.83$	6	$p<0.0001$
Low food	40.8	29.1	14.3	4.4	4.8	4.1	2.6				
High food	33.1	42.0	11.0	5.6	6.3	1.5	0.7				
Size class 4								1414	$X^2=63.50$	6	$p<0.0001$
Low food	45.5	22.3	14.4	5.6	4.9	5.1	2.2				
High food	32.3	39.7	9.8	4.9	7.7	4.3	1.3				

Figure 1. Effect of initial burrow density and food availability on burrowing activity of Uca rapax (all crabs) (N=17). Bars represent 1.96 standard error (95 % confidence intervals).


Total new burrows
New branched burrows
New unbranched burrows
All maintained branches
All maintained burrows
Branches of initial burrows
BURROWS AND BRANCHES
50
40
30
20
10
EXCAVATED SEDIMENT (g)
60
40
20
BRANCHING RATIO
1.5
1.0
0.5
BURROW DEPTH
6
4
2
% TIME BURROWING
8
6
4
2
LOW LOW
LOW HIGH
HIGH LOW
HIGH HIGH
FOOD DENSITY

(presumably in search of food), and agonistic encounters were more frequent than in high-food arenas.

Comparison of burrowing by crabs of each sex

There was no overall difference between females and males in the percent of unbranched burrows or branching ratio of burrows. However, females were less active at the surface, allocated different amounts of time to various activities, spent significantly more time burrowing, and burrowed less deeply (Tables VII and IIb). Males constructed more shelters than did females (Table VIII), and allocated significantly more time to agonism ($F=27.47$, $df=1$, $p<0.0001$, $N=53$) and to display ($F=14.56$, $df=1$, $p<0.0004$, $N=53$) (Table IIb).

Response of crabs of each sex to initial burrow density

The three-level interaction between food, burrow density, and sex, as well as the two-level interactions between pairs of these factors, were not significant for all variables examined by ANOVAs.

The effect of initial burrow density did not differ between males and females with respect to burrow configuration, branching ratio, depth, or time allocation to different activities, or to burrowing in particular. This is suggested by a qualitative comparison between the two sexes in Tables IX and IVb, and by the non-significant interaction between sex and burrow density for each variable examined. However, in arenas with a lower initial burrow density, the trend for allocating a higher fraction of time to burrowing was stronger for females.

Table VII. Comparison of burrowing activity by each sex of Uca rapax.

Variable	Females	Males	N	Test	df	Significance
% unbranched burrows	64.94 %	66.53 %	1391	X^2=0.13	1	NS
Branching ratio	1.38± 0.58	1.37± 0.59	1385	F= 0.12	1	NS (1)
Burrow depth (cm)	6.04± 2.71	6.60± 2.83	1142	F=12.46	1	p<0.0004 (1)
Activity at surface	0.69	1.40	4493	X^2=560.88	1	p<0.001
% time burrowing	9.78 %	4.33 %	53	F= 4.33	1	p<0.04 (2)

(1) Log-transformed data.
(2) Arcsine-transformed data.

Table VIII. Fraction of the total numbers of shelters constructed by Uca rapax, for each sex and each size class. The interaction between sex and size was not significant.

	%	N	Test	df	Significance
		64	$X^2=36.04$	1	$p<0.0001$
Females	18.8				
Males	81.3				
		62	$X^2=51.48$	3	$p<0.0001$
Size class 1	12.9				
2	9.7				
3	29.0				
4	48.4				

Table IX. Response of burrowing activity by each sex of *Uca rapax* to initial burrow density.

Variable	Low density	High density	N	Test	df	Significance
(a) Females						
% unbranched burrows	64.62 %	65.85 %	653	X^2=0.11	1	NS
Branching ratio	1.40± 0.57	1.37± 0.54	653	F= 0.27	1	NS (1)
Burrow depth (cm)	6.03± 2.76	6.07± 2.64	532	F= 0.21	1	NS (1)
% time burrowing	12.72 %	5.79 %	26	F= 3.27	1	NS (2)
(b) Males						
% unbranched burrows	65.05 %	68.82 %	732	X^2=1.17	1	NS
Branching ratio	1.40± 0.59	1.35± 0.55	732	F= 1.63	1	NS (1)
Burrow depth (cm)	6.44± 2.62	6.82± 3.06	610	F= 2.30	1	NS (1)
% time burrowing	5.33 %	3.09 %	27	F= 2.02	1	NS (2)

(1) Log-transformed data.
(2) Arcsine-transformed data.

Response of crabs of each sex to food availability

Crabs of the two sexes were not affected differently by food availability, with respect to percent of unbranched burrows, branching ratio, depth, time allocation to different activities, or fraction of time allocated to burrowing (Tables X and VIb). This is suggested by a qualitative comparison between the two sexes in Tables X and VIb, and by the non-significant interaction between sex and food for each variable examined.

Comparison of burrowing by crabs of different size

There was no overall difference between crabs of different sizes in the percent of unbranched burrows or branching ratio of burrows (Table XI). Smaller crabs were less active at the surface, allocated different amounts of time to various activities and burrowed less deeply (Tables IX and IIc). There was a strong trend for a higher time investment in burrowing by smaller crabs. Larger crabs constructed more shelters than did smaller crabs (Table VIII), and allocated significantly more time to agonism ($F=9.24$, $df=3$, $p<0.0001$, $N=108$) and to display ($F=4.51$, $df=3$, $p<0.005$, $N=108$). There was a strong trend for a higher time expenditure in foraging for the smaller size classes.

Table X. Response of burrowing activity by each sex of *Uca rapax* to food availability.

Variable	Low food	High food	N	Test	df	Significance
(a) Females						
% unbranched burrows	57.93 %	71.80 %	653	X^2=13.82	1	p<0.0001
Branching ratio	1.46± 0.57	1.32± 0.54	653	F=11.15	1	p<0.0009 (1)
Burrow depth (cm)	5.68± 2.44	6.38± 2.87	532	F= 7.34	1	p<0.007 (1)
% time burrowing	10.43 %	9.24 %	26	F= 0.15	1	NS (2)
(b) Males						
% unbranched burrows	60.72 %	72.65 %	732	X^2=11.74	1	p<0.001
Branching ratio	1.45± 0.61	1.30± 0.52	732	F=13.06	1	p<0.0003 (1)
Burrow depth (cm)	6.07± 2.37	7.11± 3.12	610	F=15.70	1	p<0.0001 (1)
% time burrowing	4.18 %	4.48 %	27	F= 0.30	1	NS (2)

(1) Log-transformed data.
(2) Arcsine-transformed data.

Table XI. Comparison of burrowing activity by *Uca rapax* of different sizes.

Variable	Size class 1	Size class 2	Size class 3	Size class 4	N	Test	df	Significance	
% unbranched burrows	68.73 %	61.47 %	65.70 %	69.41 %	1399	X^2=6.17	3	NS	
Branching ratio	1.31± 0.54	1.43± 0.58	1.39± 0.60	1.35± 0.59	1393	F= 2.21	3	NS	(1)
Burrow depth (cm)	5.07± 2.03	5.48± 2.15	6.87± 2.79	8.06± 3.18	1149	F=63.99	3	$p<0.0001$	(1)
Activity at surface	0.10	0.20	0.39	0.31	4536	X^2=1573.78	3	$p<0.0001$	
% time burrowing	12.56 %	6.31 %	3.83 %	5.31 %	108	F= 1.44	3	NS	(2)

(1) Log-transformed data.
(2) Arcsine-transformed data.

Response of crabs of different size to initial burrow density

The three-level interaction between food, burrow density, and size, as well as the two-level interactions between pairs of these factors, were not significant for most variables examined by ANOVAs. It was significant ($F=2.11$, $df=3$, $p<0.1$, $N=255$) for the interaction of size with initial burrow density for the percent of unbranched burrows.

Crabs of different sizes were affected differently by initial burrow density (Tables XII and IVc). This is suggested by a qualitative comparison between size classes in Tables XII and IVc, and by the significant interaction between size and burrow density for the percent of unbranched burrows. In arenas with a lower initial burrow density, for crabs of the smallest size class, branching ratio and burrow depth were significantly lower; the time allocation to burrowing and other activities was not affected by the treatment. For some of the larger crabs, time allocation to various activities was significantly affected by the treatment; the fraction of time allocated to burrowing was higher in arenas with a lower initial burrow density. No differences occurred for branching ratio and depth.

Response of crabs of different size to food availability

Crabs of different sizes were affected differently by food availability (Tables XIII and VIc). This is suggested by a qualitative comparison between size classes in Tables XIII and VIc. However, variance was high, and the interaction between size and food availability was not significant for any variable

Table XII. Response of burrowing activity by *Uca pugnax* of different sizes to initial burrow density.

Variable	Low density	High density	N	Test	df	Significance
(a) Size class 1						
% unbranched burrows	64.00 %	74.68 %	304	$X^2=4.08$	1	$p<0.0043$
Branching ratio	1.39 ± 0.54	1.40 ± 0.55	304	F= 3.88	1	$p<0.0497$ (1)
Burrow depth (cm)	4.72 ± 1.92	5.39 ± 2.05	226	F= 6.63	1	$p<0.0106$ (1)
% time burrowing	11.48 %	13.72 %	27	F= 0.01	1	NS (2)
(b) Size class 2						
% unbranched burrows	60.28 %	62.98 %	422	$X^2=0.32$	1	NS
Branching ratio	1.46 ± 0.61	1.40 ± 0.55	422	F= 0.87	1	NS (1)
Burrow depth (cm)	5.59 ± 2.32	5.36 ± 1.96	345	F= 0.17	1	NS (1)
% time burrowing	9.63 %	2.74 %	27	F= 5.13	1	$p<0.03$ (2)
(c) Size class 3						
% unbranched burrows	66.07 %	65.61 %	413	$X^2=0.01$	1	NS
Branching ratio	1.40 ± 0.60	1.38 ± 0.56	413	F= 0.04	1	NS (1)
Burrow depth (cm)	6.71 ± 2.56	7.10 ± 3.00	350	F= 1.00	1	NS (1)
% time burrowing	3.12 %	4.60 %	27	F= 0.02	1	NS (2)
(d) Size class 4						
% unbranched burrows	70.59 %	68.64 %	254	$X^2=0.11$	1	NS
Branching ratio	1.33 ± 0.55	1.37 ± 0.60	254	F= 0.28	1	NS (1)
Burrow depth (cm)	7.93 ± 2.88	8.26 ± 3.47	225	F= 0.18	1	NS (1)
% time burrowing	7.21 %	3.55 %	27	F= 1.46	1	NS (2)

(1) Log-transformed data.
(2) Arcsine-transformed data.

Table XIII. Response of burrowing by Uca rapax of different sizes to food availability.

Variable	Low food	High food	N	Test	df	Significance
(a) Size class 1						
% unbranched burrows	57.14 %	79.88 %	304	$X^2=18.39$	1	$p<0.0001$
Branching ratio	1.46 ± 0.55	1.22 ± 0.46	304	F=17.76	1	$p<0.0001$ (1)
Burrow depth (cm)	4.61 ± 1.82	5.42 ± 2.10	226	F= 8.60	1	$p<0.0037$ (1)
% time burrowing	5.01 %	20.69 %	27	F= 2.82	1	NS (2)
(b) Size class 2						
% unbranched burrows	54.71 %	69.35 %	422	$X^2=9.53$	1	$p<0.002$
Branching ratio	1.51 ± 0.60	1.34 ± 0.54	422	F= 9.16	1	$p<0.0026$ (1)
Burrow depth (cm)	5.27 ± 2.05	5.75 ± 2.24	346	F= 3.55	1	NS (1)
% time burrowing	8.94 %	5.21 %	21	F= 0.04	1	NS (2)
(c) Size class 3						
% unbranched burrows	62.83 %	68.47 %	413	$X^2=1.45$	1	NS
Branching ratio	1.42 ± 0.58	1.36 ± 0.58	413	F= 1.04	1	NS (1)
Burrow depth (cm)	6.47 ± 2.47	7.24 ± 2.96	350	F= 4.99	1	$p<0.0261$ (1)
% time burrowing	3.94 %	3.72 %	27	F= 0.04	1	NS (2)
(d) Size class 4						
% unbranched burrows	66.38 %	72.46 %	254	$X^2=1.10$	1	NS
Branching ratio	1.41 ± 0.62	1.30 ± 0.52	254	F= 1.79	1	NS (1)
Burrow depth (cm)	7.38 ± 2.40	8.66 ± 3.58	226	F= 6.20	1	NS (1)
% time burrowing	4.61 %	6.07 %	27	F= 0.10	1	NS (2)

(1) Log-transformed data.
(2) Arcsine-transformed data.

examined. In arenas with a lower food availability, for size classes 1 and 2, branching ratio was higher, and burrow depth was lower (although the difference was not significant in size class 2). For size class 3, burrow depth was also significantly lower. No differences occurred between treatments for the largest size class.

DISCUSSION

Burrow/crab Ratios in the Salt Marsh

The burrow/crab ratio was found to be higher than 1; thus, there were excess burrows. Burrow/crab ratios higher than one have been found in previous studies. Both male and female crabs dig new burrows with each tidal cycle. Burrows are relatively stable in a muddy substrate with a root mat, particularly in the medium *Spartina* zone. When abandoned, they persist through several tidal cycles (Powers, 1973; Crane, 1975; Basan and Frey, 1977; Hyatt and Salmon, 1977; Katz, 1980; Bertness and Miller, 1984).

Spartina shoot density and biomass, and sediment organic content were reasonably high though comparable to values for other medium *Spartina* marshes (Kurz and Wagner, 1957; Basan and Frey, 1977; Cammen *et al.*, 1980; Gosselink *et al.*, 1984) and root mat density was relatively low (C.S. Hopkinson, pers. comm.). Sediment water content was very similar to that found in a salt marsh in Georgia, and indicative of a relatively firm substrate and high burrow holding capacity (Teal and Kanwisher, 1961; Kraeuter and Wolf, 1974; Bertness and Miller, 1984). All these characteristics, together with a low degree of burrow intersection (discussed below; see also Basan and Frey, 1977) are "typical" of medium *Spartina* marshes. These characteristics should allow variations in crab burrowing activity in response to food supply, because they help maintain a high enough Uca population density to have a significant impact on Spartina. Furthermore, burrows in this type of substrate may last long enough to help maintain a burrow/crab ratio >1 and help enhance Spartina growth.

Uca rapax density was reasonably high compared to reported densities (Allen and Curran, 1974; Wolf et al., 1975; Aspey, 1978; Katz, 1980; Montague et al., 1981; Bertness and Miller, 1984; Cammen et al., 1984). The sex ratio (M/F) was 0.79. Sex ratios higher than 1 are often observed (Wolf et al., 1975; Bertness and Miller, 1984; Genoni, 1985), but this may be due partly to sampling biases, as females often burrow more deeply than males and move closer to the water edge in the days before the release of larvae (Schwartz and Safir, 1915). There are also discrete portions of the marsh where males display (display areas; Greenspan, 1980); Bertness and Miller (1984), however, noted that sex ratios may be lower in a medium Spartina zone than in other areas of the same marsh, presumably because the difference in burrowing ability between females and males is broader in the substrate of this zone. As for size class distribution, it was more skewed toward small sizes than in the study by these authors. However, population structure can vary remarkably between seasons and years in a salt marsh (Shanholtzer, 1973; Cammen et al., 1984; Genoni, 1985).

Maximum burrow depth was found to be 11 cm, which might be an underestimate due to the limitations of the casting technique: the presence of water in burrows sometimes prevented the resin from filling them completely. Katz (1980) found burrows as deep as 15 cm, and Bertness (1985) 20 cm, a value also attained in the arenas in this study. Basan and Frey (1977) found burrows 25 cm deep. Fiddler crabs dig even more deeply in winter (Crane, 1975). The significant association of burrows with structural elements of the substrate is probably related to the relatively low root mat density, which helps reduce the probability of burrow collapse (Bertness and Miller, 1984). Burrow configurations reflected little intersection and branching, and most burrows were J-shaped, with a straight shaft, an enlarged terminal chamber and irregular walls. Other burrows were branched or interconnected. This low degree of branching and interconnection may be related to the relatively high burrow holding capacity of the substrate (Bertness and Miller, 1984), and the irregularity of walls to the protrusion of plant roots. Allen and Curran (1974), Basan and Frey (1977) and Katz (1980) give similar descriptions of configurations. These include nearly straight (J-shaped), highly sinuous shafts, Y- or U-shaped systems and more complex systems with straight shafts or U-shaped components; the complexity decreases from the marsh edge to the higher marsh. Most burrows have an enlarged lower end, where the resident crab presumably remains during the high tide or when molting or mating.

Effects of Burrow Density and Food Availability

Uca rapax also dug excess burrows. In all treatments, fiddler crabs dug new burrows despite the presence of preexisting unoccupied burrows. Additionally, they adjusted their burrowing activity to burrow density and food availability. These crabs are known to adjust their burrowing activity to a variety of conditions, such as stem density, root mat density, substrate water, ground temperature, tidal and diurnal zeitgebers, reproductive activity, threat by potential predators, season, and male display activity, itself a function of many of these factors (Zucker, 1974; Allen and Curran, 1974; Ringold, 1979; Bertness, 1985; L.W. Powers, pers. comm.). The results presented here suggest that the digging of excess burrows and burrow branches varies inversely with food availability. Thus, part of the benefit of burrowing may be to farm Spartina.

Organic content in the surface layer of untreated arenas was lower (88 %) than the average organic content in the marsh, presumably because of the lack of macroscopic detritus. Yet this value is within the range observed in the marsh. Since fiddler crabs are food limited in the medium marsh (Genoni, 1985), this value was presumed to indeed reflect a low food availability.

Average and maximum burrow depth in arenas were greater than those found in the salt marsh, but this may simply reflect a more successful casting due to a lower water content. In fact, depths observed in the arenas are comparable to the ones found in the salt marsh studies cited above. The initial depth of artificial burrows (15 cm) was presumably adequate, since crabs did not remodel to greater depths.

The significant association of burrows with structural elements is probably related to the lack of a root mat, which makes the need of structural support for burrows particularly critical. Burrow configurations were similar to those observed in the marsh, and could be assigned to the same categories described above. However, burrow walls were smoother, due to the lack of a root mat. The lack of a root mat would presumably reduce burrow longevity. However, longevity in bare sediment was found by Bertness and Miller (1984) to be in excess of 1 wk. Since each trial was ended at or before 7.5 d, results should not be significantly biased by the collapse of abandoned burrows.

Fiddler crabs allocated 5.9 % of their activity to burrowing, which is probably an underestimate due to the visual sampling technique, since burrowing activity will continue below the surface. The display activity seemed low, perhaps due to the lack of display areas in the confinement of the arenas; to insufficient time to establish display activity; to the reduced light intensity in the laboratory; or to the phase of the tidal cycle (Greenspan, 1980). Although season affects burrowing activity (Crane, 1975), this did not complicate the present study since field and laboratory experiments were conducted during the same season.

Effect of initial burrow density

Fiddler crabs dug new burrows and branches even in arenas with a high initial burrow density. A lower initial burrow density, however, resulted in a higher number of branched and unbranched burrows. There was a trend for an increase in time spent burrowing and for less deep burrows, suggesting that time for burrowing was allocated to digging new burrows and branches rather than to making existing burrows deeper. Burrows were, then, abandoned more often in low density arenas than in high density arenas, and burrow turnover was higher. This sensitivity to the existing burrow density may reflect a tendency to dig burrows wherever possible. New burrows in a substrate with a low density may be less likely to collapse, thus making excavation of new burrows beneficial to the crabs. A second reason may be a stronger competition for territories under higher burrow density. *Uca* are responsive to the presence of other crabs, and are more likely to colonize or burrow in areas with lower apparent crab densities, such as areas with vegetation cover (Bertness and Miller, 1984; Vliet, 1981). Some species, including *Uca rapax*, construct half-domes or shelters. One function of these may be to reduce their visual contact with other males, thereby reducing aggression (Zucker, 1974, 1981).

Effect of food availability

Fiddler crabs dug more burrow branches, but average burrow depth was lower, in arenas receiving no food additions. Thus, time investment in burrowing was similar, but it was allocated to digging new burrow branches rather than digging new burrows or making existing burrows deeper. Digging burrow branches near the surface may better stimulate *Spartina* growth. The physico-chemical and nutrient requirements in the upper substrate layers may be most critical to *Spartina* growth. Indeed, in the upper layer there is a higher density of roots and rhizomes (Valiela *et al.*, 1976; Howes *et al.*, 1981; Hopkinson and Schubauer, 1985), and nutrients may be more easily extracted from sediment (DeLaune and Patrick, 1980). Furthermore, in the upper layer, oxygenation by Spartina (metabolic oxidation and passive O_2 release), nutrient inputs, or burrows have a stronger effect on these parameters (Howes et al., 1981; Bertness, 1985). In addition, digging branches near the surface may better enable crabs to keep control of the original burrow, thus reducing the risk of losing it to another crab, at the same time reducing the risk of being without a burrow should the new burrow collapse or encounter some construction obstacle. These constraints may be particularly critical where food is limiting. In contrast, in the low density situation, both unbranched and branched burrows are excavated.

Comparison of burrowing by crabs of each sex

Females spent approximately half as much time outside their burrows as did males. This observation may be an artifact of the visual sampling technique, as females are actually more involved in burrowing, removing them from view. Also they are less involved in agonistic and courtship activities. Additionally, gravid females need to protect their brood. A higher burrow turnover rate may be expected for females, because (a) they have an increased food requirement (see below); (b) they may be dislodged by large males, which are less able to burrow due to their large claw (Pearse, 1914; Hyatt and Salmon, 1977; Bertness and Miller, 1984); (c) they allocate less time to agonistic and courtship activities; and (d) non-receptive females dig more if forced to interact with displaying males (L.W. Powers, pers. comm.), an artifact of the arenas.

Males burrowed more deeply and constructed more shelters, which agrees with findings of Crane (1975), Zucker (1971, 1974) and Bertness and Miller (1984).

Response of crabs of each sex to initial burrow density

In arenas with a lower initial burrow density, females dug more burrows and remained more in their burrows. Because of their higher burrowing ability, females may be more likely to take advantage of a low burrow density by digging new burrows. Females were already spending more time burrowing than males but tended to increase their burrowing time further. Males defend display territories and breeding burrows (Greenspan, 1980), and may be also sensitive to perceived population density. Indeed, most shelters were constructed by males. Because females are less involved in agonistic and courtship activities, they may respond to a high population density by digging fewer burrows and remaining more in their burrows rather than by constructing shelters as males do.

Response of crabs of each sex to food availability

There were no differences between sexes in the effect of food availability on various parameters of burrowing activity. Thus, food availability seemed to affect the two sexes equally.

Comparison of burrowing by crabs of different size

Smaller crabs were generally less active outside their burrows, which may be due partly to an artifact of the visual sampling technique, as small crabs tended to be more involved in burrowing, thus being visible less frequently, and to their being less involved in agonistic and courtship activities. A higher burrow turnover rate may be expected for smaller crabs, because (a) they have an increased food requirement, (see below), (b) they lose their burrows more often to larger, competitively dominant, crabs (Pearse, 1914; Hyatt and Salmon, 1977; Bertness and Miller, 1984); (c) they do not allocate as much time (or any at all in the case of the smallest ones) to agonistic and courtship activities; (d) burrow longevity is lower for smaller burrows when there is no root mat (Bertness and Miller, 1984); and (e) small males may dig more if forced to interact with displaying males (L.W. Powers, pers. comm.), an artifact of the arenas.

Larger crabs burrowed more deeply and constructed more shelters, which agrees with findings of Crane (1975), Zucker (1971, 1974) and Bertness and Miller (1984). Smaller crabs, even though they tended to allocate more time to burrowing, can excavate only small amounts of sediment at a time.

Response of crabs of different size to initial burrow density

Time allocation to burrowing was increased for larger crabs in arenas with a low initial burrow density, but not by smaller crabs. Smaller crabs already tend to spend more time burrowing than larger crabs and may not be able to increase their burrowing further. Rather, smaller crabs respond by burrowing less deeply and allocating their burrowing time to new burrows. In addition, sensitivity to burrow density may be particularly high in small crabs because of their relatively high population density.

Because small crabs are less involved in agonistic and courtship activities, they may respond to a high population density by digging more unbranched and branched burrows and remaining more in their burrows, rather than by reducing their time allocation to burrowing and constructing shelters as larger crabs do.

Response of crabs of different size to food availability

Smaller crabs burrowed more under low food availability, but again dug more branches rather than increasing their time allocated to burrowing. Small crabs may be particularly sensitive to food availability because they may stand more chance of deriving benefit from their investment during their lifetime; because they can invest more time in burrowing as opposed to displaying, etc.; because their better burrowing ability may allow them to better adjust their burrowing to food availability; and because their need for food may be greater for growth. Early stages are particularly sensitive to food availability: megalops larvae may select a settling substrate partly on the basis of its organic content (Crane, 1975) and early crab stages may be more limited by food supply (Genoni, 1985). Given these reasons, smaller crabs may be more efficient at farming *Spartina*. Furthermore, they constitute a large fraction of the population.

General Considerations

As with many complex biological interactions, the observed results might be attributable to secondary interactions, or to indirect cause-and-effect relationships. For example, burrowing activity might have been affected by relative differences in physical conditions or in microtopography caused by the density of initial burrows or the addition of food flakes. However, in light of what is presently known about Uca rapax burrow dynamics, the effects of their burrows on Spartina growth, in addition to the fact that they are food limited, the results would collectively suggest a farming relationship.

Although fiddler crabs are presumably capable of responding to Spartina detritus availability, the food treatment used in this study consisted, instead, of artificial food. An attempt was made at using Spartina detritus, derived from standing dead Spartina that was collected, dried, thin-cut in a hammer mill, and aged in pens in the salt marsh for 8-12 weeks. Microorganism load was measured as the gross primary production (GPP) of the microbial population: the release of CO_2 was monitored with an Infra-Red Analyzer, and GPP was calculated by adding the slopes of CO_2 concentration in the dark (community respiration) and in the light (net community production) (Soeder and Talling, 1969). Microorganism load was extremely variable (by two orders of magnitude) between samples, and therefore detritus was deemed unsuitable as a controlled food source. This also assumes that Spartina detritus, albeit limiting in quantity, provides a suitable substrate for microorganisms, which constitute the food of Uca rapax. Conversion of detritus to microbial biomass is relatively high (Gosselink and Kirby, 1974; Haines and Hanson, 1979). Indeed, it constitutes a significant portion of the diet of these crabs (Shanholtzer, 1973; Haines, 1976; Montague, 1980b). Thus, the benefit of obtaining an increased detritus supply may not be merely a by-product of their burrowing activity (Montague, 1980a). The increased investment in burrowing under low food supply may be cost-effective because of the indirect benefit accruing to the crabs.

It would be interesting to compare responses to food availability of crabs of different sizes, in the salt marsh. If small crabs are more sensitive to food limitation, and respond to low food availability by increasing their burrowing, then their burrowing activity should be inversely proportional to their organic content. Additionally, if smaller crabs are more efficient at farming Spartina, selective removal of large or small crabs should have different effects on Spartina production. The sand fiddler crab, Uca pugilator (Bosc) would provide a useful comparison, as it often occurs sympatrically with Uca rapax or Uca pugnax in salt marshes. Burrows of Uca pugilator are excavated in sandy substrates, and have usually one opening. They include short temporary burrows (that last one tidal cycle) and deep breeding burrows, the latter resembling, in their configuration, those of Uca rapax (Basan and Frey, 1977; Christy, 1982). These characteristics (short life of one kind, use for breeding of the other kind) suggest that a flexibility in adjusting time allocation to burrowing, burrow density, branching and depth may not be as high as in Uca rapax. Moreover, since this species feeds mainly on benthic algae (Miller, 1961), it presumably does not farm grass, and although it does dig excess burrows (L.W. Powers, pers. comm.), it may be predicted not to do so in response to food limitation.

APPENDIX
MORPHOMETRIC ANALYSIS OF CARAPACE AND CHELA PROPORTIONS IN *UCA RAPAX*

Morphometric analyses in decapods have generated much interest because of their relevance to many facets of life history and their taxonomic diagnostic value (Teissier, 1960; Barnes 1968; Hartnoll, 1982). Allometric constraints affect growth and reproductive output as well as many aspects of basic physiology (e.g. Miller, 1971; Savage and Sullivan, 1978; Hines, 1982). In burrowing animals such as *Uca*, they may affect burrowing behavior and mating strategies: they allow predictions of minimal burrow diameter (Bertness and Miller, 1984) or largest mate (*Uca rapax* breed in the male's burrow; Greenspan, 1980).

This morphometric analysis correlates the basic measurements, carapace breadth (or width) and carapace length (or depth). Carapace breadth is often used as the reference dimension for morphometric studies in brachyurans (see e.g. Barnes, 1968; Hines, 1982; Davidson and Marsden, 1987). However, in the case of *Uca*, carapace length is more satisfactory (Miller, 1971; Crane, 1975). I have used both of these dimensions. The development of the major cheliped in males and its role in territorial defence, combat, display and courtship, are of special interest in fiddler crabs (Crane, 1975). Indeed it is a useful measurement for associating male size to mate size and for predicting mating success of males (Miller, 1971;

Greenspan, 1980). Regressions of propodus length and dactylus length against carapace breadth and length were calculated. The slopes and elevations of regression lines were compared between the two sexes.

The analysis includes 330 males and 308 female Uca rapax, ranging from 4.50 to 21.50 mm in carapace breadth. Carapace breadth (CB), carapace length (CL), propodus length (PL) and dactylus length (DL) were measured with vernier calipers to the nearest 0.05 mm. CB was measured across the long axis of the carapace at its maximum breadth; CL was measured medially along the minor axis of the carapace, from the front to the posterior margin; PL was measured along its lower margin, from the articulation with the carpus to the tip of the immovable digit; and DL from the articulation point on the propodus to the tip (Crane, 1975). Linear regressions are good approximations of correlations between dimensions of similar magnitude (Hartnoll, 1982). Linear regressions of the form $y=ax+b$, where y is the dependent variable, x the reference variable, and a and b are constants (Sokal and Rohlf, 1969) were done for CB vs. CL and CL vs. CB for females and males. Because the growth of the major cheliped in males is likely to follow a power function of the form $y=ax^b$ (Hartnoll, 1982), regressions of log(PL) and of corresponding power function was derived. The adjusted coefficient of determination (r^2) and the standard error on the estimate of the slope were calculated. Sexual differences in slope and elevation between regression lines were compared by t-tests (Zar, 1974).

The relationships between carapace breadth and length approximate closely straight lines (Figures 2 and 3) while the ratio of male chela measurements to carapace breadth and length follows a logarithmic straight line (Figures 4 and 5), as in some other Ocypodidae (Barnes, 1968) (Table XIV). Similarly, the carapace breadth is proportionally larger in larger individuals. It can also be noted from comparisons of the standard errors on the estimates of slopes that for any given carapace breadth, the size of the male chela shows a greater variation than carapace length.

Regressions for carapace measurements of females and males were significantly different in slope and elevation ($t=4.947$ and 5.945 respectively, $p<0.001$, $df=635$).

Comparison of the standard errors on the estimates of the slopes suggest that the measurement for the major cheliped exhibit more variation than carapace measurements. This may be due entirely or in part to smaller, regenerating chelipeds in some individuals, and has been observed in other Ocypodidae (Barnes, 1968). However, the range and rate of change of these morphometric proportions may have taxonomic or biogeographical significance (Barnes, 1968).

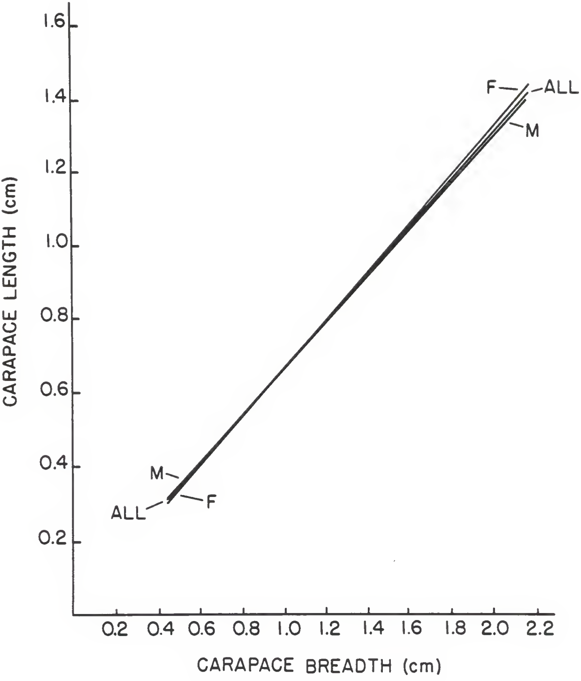


Figure 2. Regression of carapace length against carapace breadth for *Uca rapax*. F=females, M=males, ALL=All crabs.

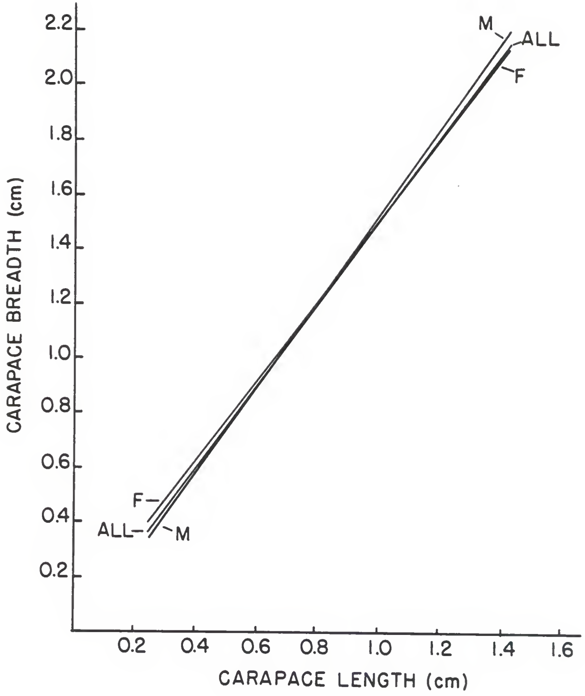


Figure 3. Regression of carapace breadth against carapace length for Uca rapax. F=females, M=males, ALL=all crabs.

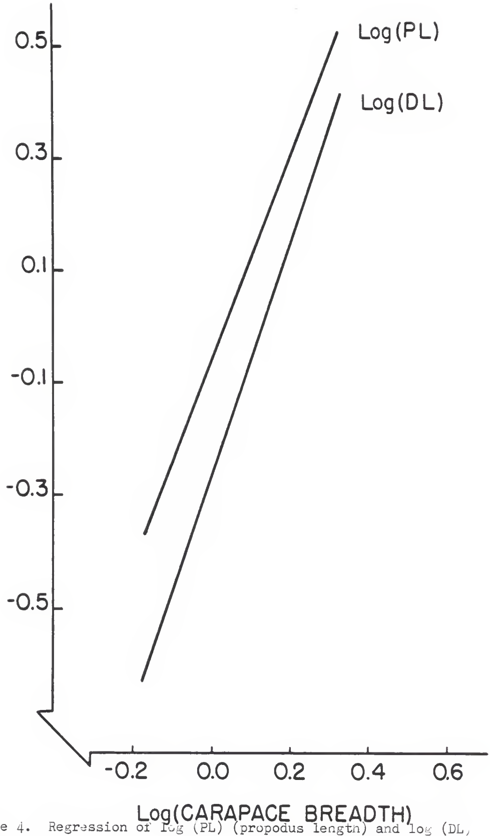


Figure 4. Regression of log (PL) (propodus length) and log (DL) (dactylus length) against log (CB) (carapace breadth) for *Uca rapax*.

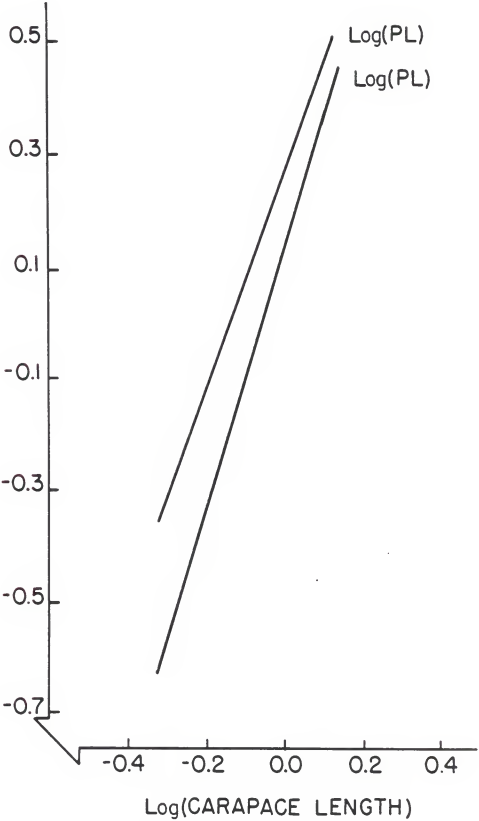


Figure 5. Regression of log (PL) (propodus length) and log (DL) (dactylus length) against log (CL) (carapace length) for *Uca rapax*.

Table XIV. Summary of allometric relationships for carapace breadth (CB), carapace length (CL), propodus length (PL) and dactylus length (DL) of *Uca rapax*. s.e.=standard error of estimate on the slope.

Sex	Variables	Type of regression	Growth equation	s.e.	r^2	N
F	CL vs. CB	linear	y=0.6504x+0.0245	0.007	0.9691	308
M			y=0.6253x+0.0418	0.005	0.9783	330
All			y=0.6330x+0.0378	0.004	0.9739	638
F	CB vs. CL	linear	y=1.4901x-0.0030	0.015	0.9690	308
M			y=1.5645x-0.0394	0.013	0.9783	330
All			y=1.5386x-0.0282	0.010	0.9739	638
M	PL vs. CB	power	$y=1.8416x^{-0.0451}$	0.055	0.9339	79
M	PL vs. CL	power	$y=1.9680x^{0.2840}$	0.063	0.9236	79
M	DL vs. CB	power	$y=2.1156x^{-0.2607}$	0.064	0.9360	79
M	DL vs. CL	power	$y=2.2596x^{0.1172}$	0.073	0.9247	79

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BIOGRAPHICAL SKETCH

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Frank J S Maturo, Jr

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